

INTER-AMERICAN TROPICAL TUNA COMMISSION COMISION INTERAMERICANA DEL ATUN TROPICAL

Bulletin — Boletín
Vol. I, No. 2



SOME ASPECTS OF THE DYNAMICS OF POPULATIONS
IMPORTANT TO THE MANAGEMENT OF THE
COMMERCIAL MARINE FISHERIES

by
MILNER B. SCHAEFER

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La Jolla, California

1954

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Introduction

A population of oceanic fish under exploitation by a fishery may be influenced by a great number of elements in the complex ecological system of which it forms a part. Of these, however, only one, predation by man, is capable of being controlled or modified to any significant degree by man's actions. Any management or control of the fishery, to the extent this may be possible at all, must, therefore, be effected through control of the activities of the fishermen. It seems important to elucidate some of the basic principles of the effect of fishing on a fish population and, conversely, the effect of the fish population on the amount of fishing, in order to understand in what circumstances and in what manner such control of the activities of the fishermen can influence the fish population and the yield obtained therefrom.

Management of a fishery has as its purpose the modification or limitation of the activities of the fishermen in order to realize a change in the fish population, or the catch, or both, which in some manner is preferable to that which would obtain if the fishermen were allowed to operate without these modifications or limitations. What may be "preferable" involves in the general case a great many economic and sociological matters difficult or impossible to treat objectively, and not susceptible to quantitative reasoning. We must, therefore, confine our attention to a less general case, but one most often met in practice, where the purpose of management is to obtain a larger average total catch per unit of time than would be obtained without management. An important special case of this is management directed toward obtaining the maximum average total catch per unit of time, which is often referred to, somewhat ambiguously, as the "optimum catch."

The Inter-American Tropical Tuna Commission has the task, specified by the Convention under which it is organized, of gathering and interpreting factual information to facilitate maintaining the populations of the tropical tunas and of the tuna-bait fishes at levels which will permit maximum sustained catches year after year. Information respecting these populations is not at the present time adequate for this purpose. An analysis of the fundamental relationships between population size, intensity of fishing, and catch is a valuable, if not indispensable, basis upon which to plan the efficient collection and interpretation of the information required to accomplish the purposes of the Commission.

The staff of the Commission has directed a large share of its attention since its inception to the collection and compilation of reliable data respecting the total catch and catch per unit of fishing effort of each tuna species over the period of growth and development of the fishery in the Eastern Tropical Pacific. This task is nearing completion. The next step in the investigation is to employ these data together with such ancillary vital

statistics as may be required and may be obtainable, to the estimation of the level of maximum sustained yield of each tuna stock and the determination of the present condition of the fishery with relation thereto. This step requires the employment of a suitable mathematical model describing the effect of fishing on the tuna stocks. Models which have been applied in the past to other fisheries are not satisfactory for this purpose. It has, therefore, proven necessary to undertake the investigations reported in this paper directed toward the development of a suitable model, and of methods of its application to fisheries data, which can be applied to the data of the tuna fishery. These studies, although of a theoretical nature, are of the most direct practical importance to the objectives of the Commission, since they are fundamental to the interpretation of the catch data and related information being collected by the staff.

It is well known that in dealing with oceanic fisheries we have to do with very complex ecological systems and that, therefore, the effects of the amount of fishing on the size of the fish population and on the catch is difficult to estimate. Some recent and current controversies bear adequate witness to this. The very complexity of these systems tends, however, to divert attention from consideration of the fundamental laws of population growth which make it possible for a species to survive increases in predator populations, and, by the same token, make possible that extensive predation by man which is commercial fishing.

In this investigation it will be attempted to indicate the manner in which the fundamental laws of population growth operate in the case of a commercial fishery, and so, perhaps, clarify some of the important considerations basic to the management of the oceanic fisheries. These will be shown by means of mathematical models. Certain parts of these models or very similar ones have been employed in predator-prey investigations of other organisms (Gause 1934, Lotka 1925), and there have been limited attempts to apply somewhat similar techniques to the fisheries, as will be noted subsequently. There is rather good reason to believe that the models sufficiently describe reality to be useful in furthering our understanding.

In pursuing the investigation we wish to elucidate the dynamics of a population of oceanic fish not related to environmental variations, that is the dynamics of the "mean" population under average environmental conditions. We shall, therefore, consider the situation in which all the factors of the environment are constant except predation by man, i.e. the amount of fishing. In application, the effect of variation due to environmental changes is treated as a random variable, independent of size of population.

The law of population growth in populations which tend to stability

Populations of organisms living in a constant environment with a limited food supply may be of one of two kinds. In one kind of population, exemplified in particular by some insects, different stages of which are in

competition with each other for the means of life, the number of adults fluctuates periodically and continuously (Nicholson 1949, 1950). In the other type, the population tends to stability, so that for a particular set of environmental conditions the population has at each size a definite potential rate of increase which is dependent only on the existing size of the population. A great many populations from the yeasts and protozoa to man have been shown to be of this sort. Most, at least, of the populations of fishes are believed to be of this kind.*

The general law of population growth for such a population, P , may be expressed as

$$\frac{dP}{dt} = f(P) \dots\dots\dots (1)$$

where $f(P)$ is continuous, positive and single valued between $P = 0$ and $P = L$, the maximum population which the living space and food supply can support, and zero at these limiting values of P . We will call $f(P)$ the *natural rate of increase*.

A particular function which has been shown to fit experimental data as well as data from populations in nature for a good many organisms is the Verhulst-Pearl logistic

$$\frac{dP}{dt} = k_1 P(L - P) \dots\dots\dots (2)$$

where k_1 is a constant

In this case, of course, $f(P)$ is a parabola with its axis along $P = L/2$. It is shown graphically in Figure 1. Integrating, we may obtain P as a function of t , which is a sigmoid curve with an upper asymptote at $P = L$ and an inflection point at the value of P for which $\frac{dP}{dt}$ is a maximum, i.e. at $P = L/2$.

This law has been employed to describe the growth of a considerable variety of organisms, for example yeasts (Gause 1934, p. 78, Pearl 1925, p. 9), protozoa (Gause 1934, p. 36, p. 93 et. seq.), fruitflies (Pearl 1925, p. 11), and humans (Pearl 1925).

Büchman (1938) has considered the general dynamics of commercial fish populations based on this relationship, as has Graham (1939). Graham (1935) employed this growth law in an analysis of the effect of World War I on the abundance and landings of demersal fishes from the North Sea, and Baerends (1947) has made similar analyses.

It is possible that for fish populations the special case of (1) represented by the logistic (2) is not, in general, an exact representation of the

*One notable exception may be some species of Pacific Salmon, which tend to periodic fluctuations characteristic of the species. These may be found to be the result of the direct or indirect competition of different year classes for the means of subsistence. This has been little investigated, however.

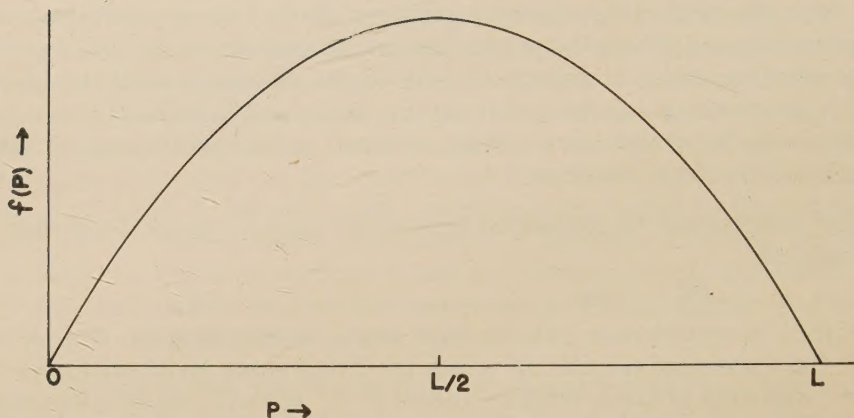


Figure 1. Natural rate of increase of a population which grows according to the Verhulst-Pearl logistic.

population growth law. In particular, the relationship (2) is a parabola, symmetrical with respect to its axis, from which it follows that the maximum natural rate of increase occurs at a value of P half way between zero and the maximum population value, L . There is reason to believe that in at least some populations of fishes, the curve is actually somewhat asymmetrical, with the maximum value of $\frac{dP}{dt}$ at a value of P less than $L/2$. Experimental data have also shown this is sometimes the case for other organisms, for example the yeast data of Gause (1934, p. 68).

Effects of Fishing

A fishery, that is removal of fish from the stock by man, has the effect of subtracting from that increase in stock which would occur at the existing level of population if no fishing were taking place. In other words, the rate of change in the stock will be less than the natural rate of increase by an amount equal to the rate of catching of the fish. That is

$$\frac{dP}{dt} = f(P) - P \phi(F) \dots\dots\dots (3)$$

where $P \phi(F)$ is the *rate of catching*, depending on the size of the fish stock and some positive single valued function of the number of units of fishing effort, F .

It is obvious from (3) that whenever the rate of catching is less than the natural rate of increase, the population will increase. Conversely, when the rate of catching exceeds the natural rate of increase, the population shrinks in size. When the rate of catching is exactly equal to the natural rate of increase, $\frac{dP}{dt} = 0$, the population remains unchanged, and the fishery is said to be in equilibrium for that level of population and fishing effort. The annual catch made under such a condition of equilibrium has been

called the stabilized catch, the equilibrium yield, and other things. We shall call it the *equilibrium catch*.

From the equation (3) and the general form of $f(P)$ certain conclusions of importance in fishery research and management may be immediately perceived:

(1) As the fishery increases in intensity (as F increases), the stock P , decreases. This decrease in population is a necessary consequence of increasing fishing intensity, and, thus, is an inevitable result of the development of a fishery.

(2) The stock, and the corresponding equilibrium catch, can be held constant, by regulating the amount of fishing, at any value less than $P = L$. Stability or instability of the population and catch over a given period of time has, therefore, no necessary relationship to the level of abundance, but merely reflects whether the rate of catching is changing or is constant.

Catch per unit of effort

Let it be assumed that the fishery operates on the stock in such a manner that one unit of fishing effort produces the same relative effect on the stock, that is it catches the same percentage of the stock, regardless of the time or place it is applied. Then

$$\phi(F) = k_2 F \quad \text{where } k_2 \text{ is a constant}$$

$$\text{and } P \phi(F) = k_2 P F \dots\dots\dots (4)$$

Under these circumstances, the rate of catching per unit of fishing effort is

$$\frac{k_2 P F}{F} = k_2 P \dots\dots\dots (5)$$

and is, thus, proportional to the stock. The average catch per unit of effort during a given period of time will be proportional to the average size of the fish stock encountered by the fishery during the period. The average catch per unit of effort per year, or some other short time period, has been extensively used by fishery scientists to measure changes in the size of fish populations.

Maximum equilibrium catch

As has been shown above, when the rate of catching is just equal to the natural rate of increase, the stock will remain unchanged and the catch obtained will, of course, be stabilized also. The size or sizes of stock at which the equilibrium catch may be maximized are levels of maximum equilibrium catch. In general, it is supposed that a fish population has a growth law at least similar to (2) in that there is but a single maximum. In this case, there is but a single size of population at which the equilibrium catch may be maximized. This size of population has been referred to as the optimum stock and the corresponding rate of catching as the optimum

catch. I prefer the expression *maximum equilibrium catch* as being more descriptive of exactly what is meant.

Determination of the status of the fish population and estimation of equilibrium yields

In the practical consideration of management of a fishery we are interested in finding out whether the fish population has been driven below the point at which maximum equilibrium catch may be obtained. If so, curtailment of the intensity of fishing will result in increased average catches. It is also of interest to estimate, if possible, the maximum equilibrium catch and the size of population at which it may be obtained.

The investigation of these matters involves, essentially, estimating the equilibrium catch at various levels of population. This may be accomplished by application of equations (3) and (4) where the assumptions underlying these equations are sufficiently nearly realized.

From (3) and (4) we have

$$\frac{dP}{dt} = f(P) - k_2PF \dots \dots \dots (6)$$

Integrating over the year, we obtain

$$\int_{P_0}^{P_1} dP = \int_0^1 f(P)dt - \int_0^1 k_2PFdt \dots \dots \dots (7)$$

where $P = P_0$ at $t = t_0$

and $P = P_1$ at $t = t_1$

from which

$$P_1 - P_0 = \Delta P = \overline{f(P)} - k_2F_t\overline{P} \dots \dots \dots (8)$$

Where $\overline{f(P)}$ is the annual natural rate of increase and, hence, the annual equilibrium catch corresponding to the mean stock $\overline{P}$ encountered by the fishery during the year*. F_t is the total fishing intensity for the year, $F_t = \int_0^1 Fdt$. $k_2F_t\overline{P}$ is, of course, the total catch during the year.

The average catch per unit of effort is

$$U = \frac{k_2F_t\overline{P}}{F_t} = k_2\overline{P} \dots \dots \dots (9)$$

If we have adequate statistical records of the fishery we know the amount of effort, the catch, and the catch per unit of effort year-by-year. If we can evaluate k_2 in (9) we shall be able to compute $\overline{P}$ for each year from the catch statistical data. From values of $\overline{P}$ we may estimate P_1 and P_0

* $\overline{P}$ is the average of P taken with respect to the units of effort applied during the year.

$$\text{That is, } \overline{P} = \frac{\int_0^1 PFdt}{\int_0^1 Fdt}$$

approximately by interpolating between values of $\bar{P}$ for successive years. Given $P_t - P_0$ and the catch, we can estimate $\bar{f}(\bar{P})$, the annual equilibrium catch corresponding to $\bar{P}$ during each year of the series.

One estimate of k_2 is provided by data from tagging experiment, since $F_t k_2$ is simply the instantaneous rate of fishing mortality, that is $f = 1 - e^{-k_2 F_t}$, where f is the annual fishing mortality rate, which may be determined from the recovery rates of marked fish. Other means also exist, of course, for estimating k_2 .

An application to the Halibut fishery of the North Pacific

The manner in which this procedure may be applied can be illustrated by the example of the fishery for Pacific Halibut, using for our example the population of Area 2 (the region south of Cape Spencer). Statistics of catch and catch per unit are given by Thompson and Bell (1934) and by Thompson (1950). Revised, and presumably more accurate, values have been furnished recently by Bell to Dr. R. VanCleve (MS) from which I have taken the values employed here; see the first three columns of Table 1.

Tagging experiments (Thompson and Harrington, 1930) conducted in Area 2 indicated an annual fishing mortality rate of approximately 40% in 1926. Subsequently Thompson and Bell (1934) found that 47% was perhaps more realistic. Using 47% as the annual fishing mortality rate in 1926, we have

$$e^{-F_t k_2} = 0.53, \text{ and } F_t = 494,078 \text{ skates (Thompson 1950, table 2)}$$

Then $F_t k_2 = 0.635$

$$\text{and, } 1/k_2 = \frac{494}{0.635} \times 10^6 = 778 \times 10^3^*$$

Multiplying the values of U for each year by $1/k_2$ we obtain estimates of $\bar{P}$ (Table 1, column 4). Interpolating between successive values of $\bar{P}$, we obtain estimates of the stock at the beginning of each year (column 5). Differences of the values for successive years indicate the increase or decrease of the stock which resulted from the catch taken during the year (ΔP , column 6). In accordance with (8) we add ΔP to the annual catch to obtain $\bar{f}(\bar{P})$, the annual equilibrium catch corresponding to $\bar{P}$ (column 7).

We now have estimates of the stock and equilibrium catch obtainable from that stock for the series of years from 1916 to 1946. Plotting $\bar{f}(\bar{P})$

*By considering changes in catch per unit of effort and total catch over the period 1926 to 1933, during which period the stock fell and then returned again to the original level, Thompson (1950) arrived at a value for $1/k_2$ of 335×10^3 . This corresponds to a fishing mortality rate of about 77% in 1926, which seems unreasonably high from the tagging results, age composition data, and other information respecting this fishery. An indication of why his analysis gives this result will be given later (p. 37).

against $\bar{P}$ we would expect the points to fall on a curve (a parabola, if $f(P)$ is the logistic) in the absence of other influences. Actually, due to unknown effects of variable environmental factors, measurement errors, and other unaccounted-for sources of variation, the points will tend to scatter about an average curve. By observing the trend of the plot of $\bar{f}(\bar{P})$ against $\bar{P}$, we may ascertain, however, how the equilibrium catch for this population varies, on the average, with the size of the population. This has been done in Figure 2, where the small, solid points represent the annual values from Table 1. The centers of the crosses represent the mean values calculated for each 10 units of U .

It is quite obvious that the equilibrium catch increases, on the average, up to a catch per unit of effort of about 80 pounds per skate, at least, corresponding to a mean population of some 62,000,000 pounds. Data beyond this population level are not available (the single point for 1916 at 114 lbs. per skate is not deemed adequate for extending the relationship). Certainly it appears that, contrary to the contention of Burkenroad (1951, 1953), this halibut population was driven below its point of maximum equilibrium catch, and the curtailment of fishing had a beneficial effect on the subsequent catches.

It is unfortunate that reliable data are not available for earlier years when the population was, presumably, larger, which would enable us to estimate equilibrium catches for higher population values and so find out where the maximum occurs. It appears that it might be desirable, if possible, in order to find this out, to curtail fishing to permit higher levels of population to be reached.

This example points out clearly the desirability of obtaining adequate statistical data on a fishery during its early stages so that the maximum equilibrium catch may be estimated, approaching it from those population levels which are too high to give the maximum equilibrium catch. It is practically difficult, once the maximum has been passed, to drive the stock back up past the point of maximum return for purposes of investigation, since the immediate economic welfare of the industry must always be considered in practical regulations.

In the analysis of the halibut data thus far, we have not specified the form of $f(P)$ beyond the general restrictions on (1). As a matter of illustrating methodology, it is of interest to see what results are obtained if we specify that the curve be the logistic (page 29), so that

$$\bar{f}(\bar{P}) = k_1 \bar{P} (L - \bar{P}) \text{ or,}$$

$$\text{since } \bar{P} = \frac{U}{k_2},$$

$$\bar{f}(\bar{P}) = \frac{k_1}{k_2^2} U (L_u - U),$$

$$\text{where } L_u = k_2 L$$

Fitting a curve of this form to the mean values (crosses) of Figure 2, (with

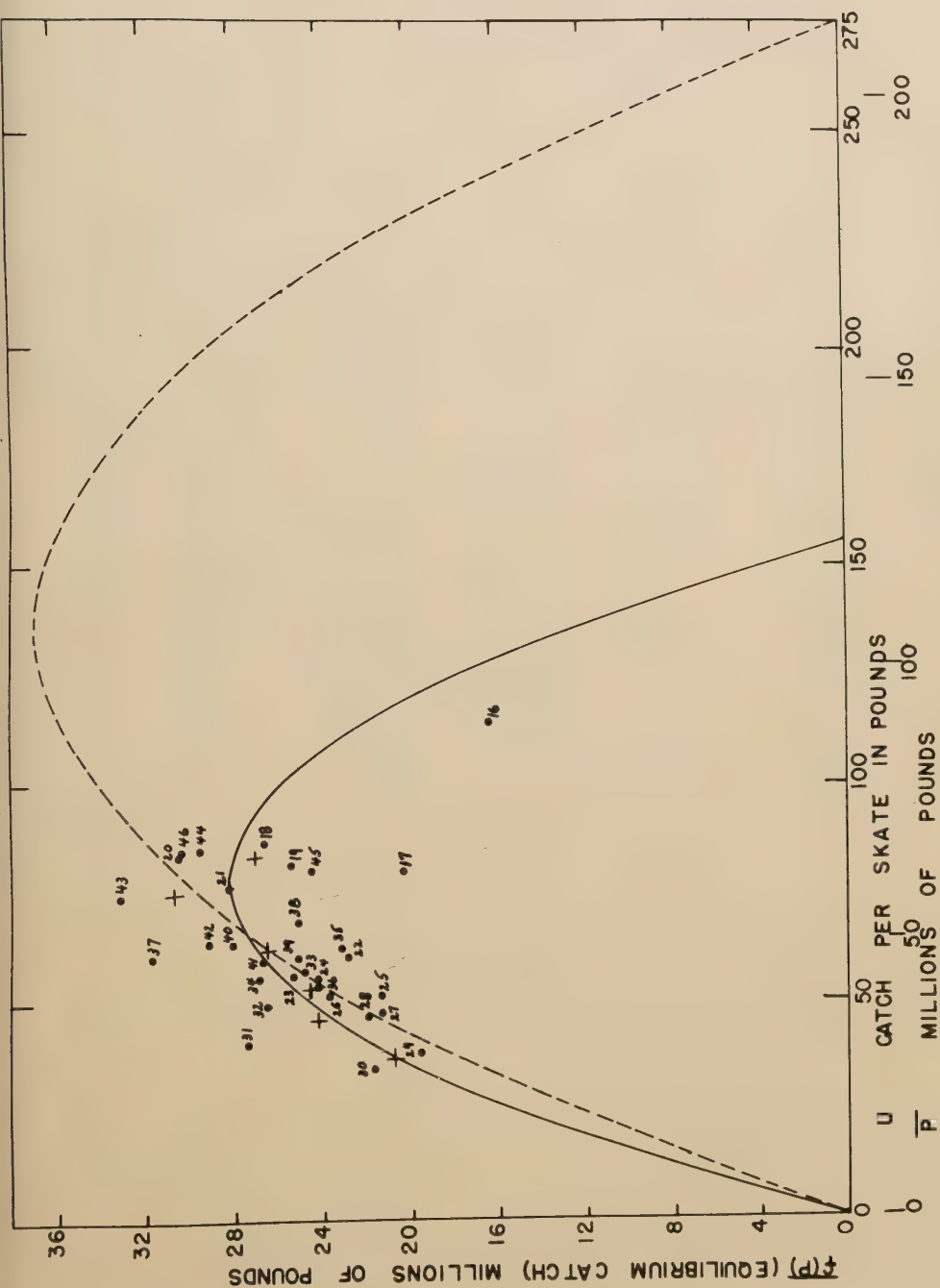


Figure 2. Relationship between mean population and estimated equilibrium catch, Pacific halibut south of Cape Spencer.

TABLE 1. Estimation of Equilibrium Catches for the Population of Pacific Halibut of the Region South of Cape Spencer (I. F. C. Area 2)

Year	Catch in 1000's of pounds ($k_2 F_1 \bar{P}$)	Catch per unit of effort in pounds per skate ($U = k_2 \bar{P}$)	$\bar{P}$	P_0	ΔP	$\bar{f}(\bar{P})$
1915	44,023	117.5	91,415			
1916	30,278	114.1	88,770	90,092	-14,082	16,196
1917	30,803	81.3	63,251	76,010	-10,542	20,261
1918	26,270	87.0	67,686	65,468	+ 195	26,465
1919	26,602	81.8	63,640	65,663	- 1,323	25,279
1920	32,358	83.6	65,041	64,340	- 2,100	30,258
1921	36,572	76.4	59,439	62,240	- 8,364	28,208
1922	30,482	62.1	48,314	53,876	- 7,663	22,819
1923	28,008	56.7	44,113	46,213	- 2,645	25,363
1924	26,155	55.3	43,023	43,568	- 2,101	24,054
1925	22,637	51.3	39,911	41,467	- 1,360	21,277
1926	24,711	51.7	40,223	40,107	- 974	23,737
1927	22,934	48.9	38,044	39,133	- 1,722	21,212
1928	25,416	47.3	36,799	37,411	- 3,530	21,886
1929	24,565	39.8	30,964	33,881	- 4,900	19,665
1930	21,387	34.7	26,997	28,981	+ 272	21,659
1931	21,627	40.5	31,509	29,253	+ 5,718	27,345
1932	21,988	49.4	38,433	34,971	+ 4,279	26,267
1933	22,530	51.5	40,067	39,250	+ 2,217	24,747
1934	22,638	55.1	42,868	41,467	+ 4,240	26,878
1935	22,817	62.4	48,547	45,707	- 311	22,506
1936	24,911	54.3	41,245	45,396	- 778	24,133
1937	26,024	60.4	46,991	44,618	+ 5,640	31,664
1938	24,975	68.8	53,526	50,258	+ 39	25,014
1939	27,354	60.5	47,069	50,297	- 2,372	24,982
1940	27,615	62.7	48,781	47,925	+ 233	27,848
1941	26,007	61.1	47,536	48,158	+ 622	26,629
1942	24,321	64.3	50,025	48,780	+ 4,707	29,028
1943	25,311	73.2	56,950	53,487	+ 7,819	33,130
1944	26,517	84.4	65,633	61,306	+ 2,840	29,357
1945	24,378	80.5	62,629	64,146	+ 39	24,417
1946	29,678	84.5	65,741	64,185	+ 2,100	31,778
1947	28,652	85.9	66,830	66,285		

$\bar{P}$ and $\bar{f}(\bar{P})$ in thousands of pounds, U in pounds per skate) under the criterion of least squares, we obtain

$$\frac{k_1}{k_2^2} = 4.64 \quad L_u = 156.1$$

This curve is plotted as the solid line in Figure 2*. It may be seen that it has a maximum value of 28.25 million pounds for the equilibrium catch at $k_2 \bar{P} = 78.05$ pounds per skate.

This curve depends, of course, only on the points to which it is fitted, and may be rather different beyond those points from the curve which would be obtained if we had some values of $\bar{f}(\bar{P})$ for higher population levels. The calculated maximum population, corresponding to 156.1 pounds

*See footnote, Page 37.

per skate, is much less than is shown by the available data of catch per skate for the early years of the fishery. From the few data available it is indicated by the International Fisheries Commission (Thompson and Bell 1934, table 1) that in the early 1900's the catch per skate was as high as 270 or 280 pounds. This is not, however, necessarily inconsistent with our results, since in the early days of the fishery the vessels may have been operating on local concentrations of halibut more abundant than the average for the entire area fished in later years. Thompson (1950, p. 2) states of the records on which these values are based: "It is my opinion, from personal experience, that such records showed a higher catch per set than the present comprehensive methods of collecting would have shown."

On the other hand, if we assume that the data from the 1900's are representative of the population in an almost unfished condition, so that the maximum population which the area will support corresponds to a catch per skate of, say, 275 pounds, we may fit a logistic to the available points, as before, but with the further restriction that $L_u = 275$. This results in a value of $k_1/k_2^2 = 1.95$. This curve is plotted as a broken line in Figure 2. It will be seen that now the estimated maximum equilibrium catch is 36.9 million pounds at a population corresponding to 137.5 pounds per skate. This result is not entirely unreasonable in the light of the total catches of 50 to 60 million pounds per year which were actually obtained by the fishery at its peak of production. (Thompson and Bell, table 1).

It is, it seems, not possible from the data to estimate precisely the population level giving the maximum equilibrium yield. We can, however, state with some certainty that it is at least as high as about 62 million pounds, corresponding to a catch per skate in the neighborhood of 80 pounds, and that at lower values the stock is overfished. This limited conclusion is, however, of very great interest in view of current controversy over the effect of regulation on the halibut stocks.

The nature of the growth of the amount of fishing

The intensity of fishing also may be expected to increase or decrease according to some regular law in response to economic factors. In general, as in any business, new investment of capital and effort will be attracted

*It may now be indicated why Thompson's method of determining $1/k_2$ gives a value higher than that from the tagging data. He assumed that the equilibrium catch for the years 1926 to 1933 was a constant. Actually the equilibrium catch was not constant over this period. The deviations of actual catches for this series of years from the equilibrium catches estimated from the logistic with the constants indicated are, on the average, greater than the deviations from the average of $\bar{f}(\bar{P})$ over the same period of years. As may be observed from Thompson's formulae on p. 20 of his paper, this will result in a higher value of his "K", which is the same as our $1/k_2$.

to come into the fishery as long as the expected return is equal to or greater than that from alternative enterprises in which the investment might be made. Put in another form, we may state this according to the theory of the "marginal" factor, according to which the cost of the last unit of fishing effort applied will, in general, be equal to the return from that unit.

Under the economic system in effect in most parts of the world, in which the above type of law holds true, as the fishery proves profitable, vessels and fishermen are attracted to it, increasing the rate of catching. This, of course, results in a decrease in the population of fish, lowering the return to each unit of fishing effort, and making the fishery less attractive to new investment. Ultimately, as the fishery grows, that level of fish population will be reached at which the return per unit of effort is so low that the cost of the next unit will be greater than the return from it. If the population falls below this level, vessels will tend to leave the fishery. This may be formulated

$$\frac{dF}{dt} = \psi(F, P - b) \dots \dots \dots (10)$$

where ψ is positive when $P > b$ and negative when $P < b$, F being, as before, the number of units of fishing effort, and b the critical level of fish population at which further investment in fishing becomes unprofitable.

To arrive at a particular function to describe the change of the intensity of fishing with the size of the population, we may consider that the incentive for new investment is proportional to the return to be expected, in which case there will be a linear relation between the percentage rate of change of fishing intensity and the difference between the level of fish population and its economically critical level, b . This function will, then, be

$$\frac{dF}{dt} = k_s F(P - b) \dots \dots \dots (11)$$

where k_s is a constant.

It may be noted that this is the law of growth of predator populations which has been arrived at in various predator-prey studies, for example Lotka (1925, p. 88), Volterra and d'Ancona (1935).

Stabilization of an unregulated fishery

Equations (3) and (10), taken simultaneously, describe the mutual interaction of a population of fish, the growth law of which is specified in (1) and a "population" of fishermen, the growth law of which is specified by equation (10). A very general model of a fishery is, then, given by the simultaneous equations

$$\left. \begin{aligned} \frac{dP}{dt} &= f(P) - P \phi(F) \\ \frac{dF}{dt} &= \psi(F, P - b) \end{aligned} \right\} \dots \dots \dots (12)$$

An important special case is a population of fish the growth law of which is the logistic, being fished under economic circumstances such that

the intensity of fishing has the growth law (11), and where the rate of catching is proportional to the number of units of fishing effort. In this case, the interaction of the fish and fishermen is described by the simultaneous equations

$$\left. \begin{aligned} \frac{dP}{dt} &= k_1 P(L - P) - k_2 PF \\ \frac{dF}{dt} &= k_3 F(P - b) \end{aligned} \right\} \dots\dots\dots (13)$$

For the reasons which have been given in previous discussion, it is believed that this pair of equations is sufficiently descriptive of the actual laws under which a commercial fishery operates to be of utility in analysis of its dynamics, and will be employed in investigation of the nature of the development of fisheries. Certain important results may be obtained, however, from consideration of the more general pair of equations (12).

As has been pointed out previously, by the first equation of (12) the population of fish and the corresponding equilibrium catch may be stabilized at any level by regulating the amount of fishing, since $\frac{dP}{dt} = 0$ whenever $f(P) = P\phi(F)$. The change in fishing intensity in an unregulated fishery will be zero, however, only at $P = b$, so that the system can only be in equilibrium naturally at $P = b$. If the system is such that it will come to a stable equilibrium at all, it will, under no regulation, reach stability of itself at the economically critical population level $P = b$.

This has implications of importance to fishery management:

(1) If b is above the value of P at which $f(P)$ is maximum, the intensity of fishing will cease to increase at a level of fish population greater than that at which the maximum equilibrium catch might be obtained. In this case regulation of the fishery cannot increase the average yield of the fishery.

(2) If b is below the value of P at which $f(P)$ is maximum, it will be possible to increase the equilibrium catch by curtailing the amount of fishing and, if sufficient information is available, to establish that rate of fishing which will result in the fish population which will give maximum equilibrium catch.

It is to be noted that the system defined by the simultaneous equations (13), which seem realistic for describing existing commercial marine fisheries, is such that it will come to stability of itself with $P = b$ and $F =$

$\frac{k_1}{k_2}(L - b)$. It will be shown later (p. 41) that this is a point of stable equilibrium. The *manner* in which it arrives at stability will also be discussed subsequently.

The course of development of an unregulated fishery and the manner of approach to stable equilibrium

It is of considerable importance to our understanding of the fisheries to investigate the manner in which the population of fish and the amount of fishing react with each other in the course of development of the fishery. We may take as our mathematical model the pair of differential equations (13) and investigate the nature of the solutions. The initial conditions, when the fishery starts, are that P is equal to L and F is small.

There does not seem to be any formal solution of these equations giving P and F as functions of time. It is possible, however, to obtain approximate solutions by means of numerical procedures. First, however, it will be profitable to investigate some of the general properties of the solutions.

By dividing the first equation of (13) by the second, we may obtain an equation in P and F .

$$\frac{dP}{dF} = \frac{k_1 P(L - P) - k_2 PF}{k_3 F(P - b)} \quad (14)$$

This equation does not have, so far as I can ascertain, a formal solution. The general nature of the solution may be investigated, however. It may be seen that there is a line of horizontal tangents, $\frac{dP}{dF} = 0$, when

$$k_1(L - P) = k_2 F, \text{ or } F = \frac{k_1}{k_2}(L - P), \quad P \neq b$$

there is a line of vertical tangents, $dF/dP = 0$

$$\text{when } P = b, \quad F \neq \frac{k_1}{k_2}(L - b)$$

At $F = \frac{k_1}{k_2}(L - b)$, $P = b$ there is a singular point.

Furthermore, it may be seen that

$$\text{when } P > b \text{ and } F > \frac{k_1}{k_2}(L - P) \quad \frac{dP}{dF} \text{ is negative}$$

$$\text{when } P > b \text{ and } F < \frac{k_1}{k_2}(L - P) \quad \frac{dP}{dF} \text{ is positive}$$

$$\text{when } P < b \text{ and } F > \frac{k_1}{k_2}(L - P) \quad \frac{dP}{dF} \text{ is positive}$$

$$\text{when } P < b \text{ and } F < \frac{k_1}{k_2}(L - P) \quad \frac{dP}{dF} \text{ is negative}$$

From this it may be seen that (14) might represent either a family of closed curves or spirals about the singular point. The corresponding solutions of (13) for P and F as functions of t are in the first case an undamped oscillatory function, and in the second a damped oscillatory function, approaching $P = b$ and $F = \frac{k_1}{k_2}(L - b)$ in the limit. In the latter case, the singular point of (14) is a point of stable equilibrium, in the former it is not.

We may examine the behaviour of the solution of (14) in the vicinity of the singular point to determine which it may be.

Lotka (1923) has investigated a more general pair of differential equations, which include ours as a special case. He has shown that if a certain discriminant is less than, equal to, or greater than zero, the solution is a spiral winding inward toward the singular point, a family of closed curves, or a spiral winding outward. (The last solution is, of course, impossible in our case from the physical conditions). The value of Lotka's discriminant " R " of our equations is

$$R = \frac{-1/2(k_2 b)^{1/2} \left[\frac{k_1 k_3}{k_2} (L - b) \right]^{-1/2}}{\frac{k_1}{k_2} (L - P)}$$

Since $(L - b)$ and $(L - P)$ are always positive in our case, R is always less than zero.

Therefore, according to Lotka's analysis, the solution would be a spiral winding inward toward the singular point. A diagram of this solution is shown in Figure 3.

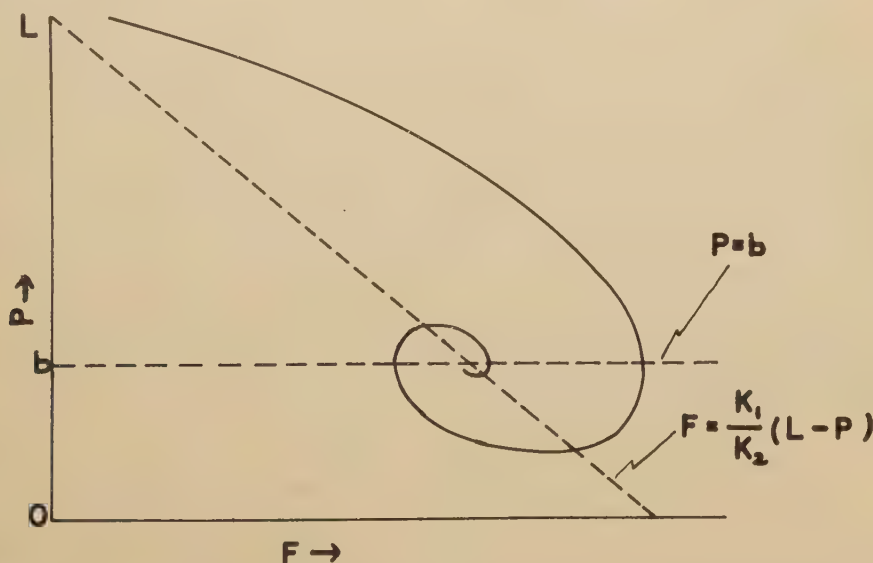


Figure 3. Solution of equation (14), according to Lotka's analysis.

It appears from this that in general P , the fish population, taken as a function of time, follows some damped oscillatory function, fluctuating above and below $P = b$, but the amplitude of the fluctuations getting smaller and smaller. Similarly F , the amount of fishing effort, follows a similar function, approaching $F = \frac{k_1}{k_2} (L - b)$ in the limit. The singular point is a

point of stable equilibrium. It is the point which F and P tend to approach, and is the only point where the unregulated fishery will stay in natural equilibrium.

We may note in passing that the line of horizontal tangents $F = \frac{k_1}{k_2}(L - P)$ is the locus of the values of F and P corresponding to the equilibrium condition, that is if we hold F constant at any given value, by regulation, the corresponding value of P lies on this line, when the catch and the natural rate of increase are in equilibrium.

The general nature of the solutions of (13) may also be investigated more directly. If we differentiate the first equation of the pair and substitute from the second, we obtain a differential equation of the second degree in P alone:

$$\frac{d^2P}{dt^2} - \frac{1}{P} \left(\frac{dP}{dt} \right)^2 + [k_1P - k_3(P - b)] \frac{dP}{dt} + k_1k_3P(P - b)(L - P) = 0 \quad (15)$$

This equation cannot, so far as I can see, be solved formally. However, we may investigate the solutions in the neighborhood of the singular point of (14). Taking a new origin at b , by taking $P = N + b$, we obtain

$$\frac{d^2N}{dt^2} = \frac{1}{N+b} \left(\frac{dN}{dt} \right)^2 - (k_1 - k_3)N \frac{dN}{dt} - k_1b \frac{dN}{dt} - k_1k_3[(L - b)bN + (L - 2b)N^2 - N^3] \quad (16)$$

In the vicinity of the origin, i.e. for very small values of N , we may neglect all terms of the second and higher degree, provided also that $\frac{dN}{dt}$ is small in the vicinity of the singular point of (14). We obtain:

$$\frac{d^2N}{dt^2} \cong -k_1b \frac{dN}{dt} - k_1k_3b(L - b)N \quad (17)$$

Or

$$\frac{d^2N}{dt^2} + k_1b \frac{dN}{dt} + k_1k_3b(L - b)N \cong 0 \quad (18)$$

which is a homogeneous linear equation with constant coefficients. The roots of the characteristic equation are

$$-k_1b \pm \frac{\sqrt{k_1^2b^2 - 4k_1k_3(L - b)b}}{2} \quad (19)$$

The form of the solution will depend on whether the roots are real or complex, i.e. whether the term under the radical is positive or negative. If the roots are complex, the solution will be of the form

$$N = e^{-\frac{k_1bt}{2}} \left(C_1 \cos \frac{a}{2}t + C_2 \sin \frac{a}{2}t \right) \quad (20)$$

where $a = \sqrt{4k_1k_3b(L - b) - k_1^2b^2}$ and C_1, C_2 are constants of integration. This solution is, of course, a damped harmonic. As $t \rightarrow \infty$, $N \rightarrow 0$, approaching the limit by oscillating above and below $N = 0$. This solution is the same kind obtained by Lotka's analysis.

On the other hand, if the roots are real, the solution will be of the form

$$N = C_1 e^{-\left(\frac{k_1 b}{2} + \frac{a}{2}\right)t} + C_2 e^{-\left(\frac{k_1 b}{2} - \frac{a}{2}\right)t} \quad \dots\dots\dots (21)$$

$$\text{where } a = \sqrt{k_1^2 b^2 - 4k_1 k_3 b(L - b)}$$

Here, as $t \rightarrow \infty$, $N \rightarrow 0$, so that the origin is a point of stability, but in this case it is approached from one side only, the equilibrium condition being approached smoothly without oscillations.

The solution will be oscillatory or not depending on whether

$$k_1^2 b^2 \begin{matrix} < \\ = \\ > \end{matrix} 4k_1 k_3 b(L - b)$$

or

$$k_1 \begin{matrix} < \\ = \\ > \end{matrix} 4k_3 \frac{(L - b)}{b} \quad \dots\dots\dots (22)$$

In the case of real roots, where the point of stable equilibrium is approached from one side only, P is always greater than b , and, correspondingly, F is always greater than $\frac{k_1}{k_2}(L - P)$. Thus, the resulting relationship between F and P , which is a solution of (14), is, in this case, not a spiral, but is a curve remaining always on the positive sides of the lines of horizontal and vertical tangents, and terminating in the limit in the singular point.

These considerations tell us something about the general nature of the solutions and their behavior near the point of stable equilibrium. In order to find out in more detail the changes in the fish population, amount of fishing, and catch, recourse may be taken to approximation methods for solving the equations (13). We have employed the method due to Lord Kelvin, as described by Willers (1948, p. 394 et. seq.) to obtain a graphical solution to the equation (15) and the corresponding equation for F as a function of t . Solutions have been computed for two examples, one of which has complex roots and one of which has real roots for equation (18).

In the first example we have taken

$$\begin{array}{ll} k_1 = k_3 & b = 0.3L \\ \text{initial conditions, } P = L & F = 0.1 \end{array}$$

The resulting solution, showing F and P as functions of t , is traced out in Figure 4. It may be seen that the fish population and the intensity of fishing approach the condition of stable equilibrium as a series of damped oscillations. The catch, which is proportional to the product of F and P , also oscillates about its point of stable equilibrium, as may be seen from the graph of catch in the same figure. It is of interest to note that on the first swing the catch rises far above its ultimate position of stable equilibrium, and also above the level of maximum equilibrium catch, which also

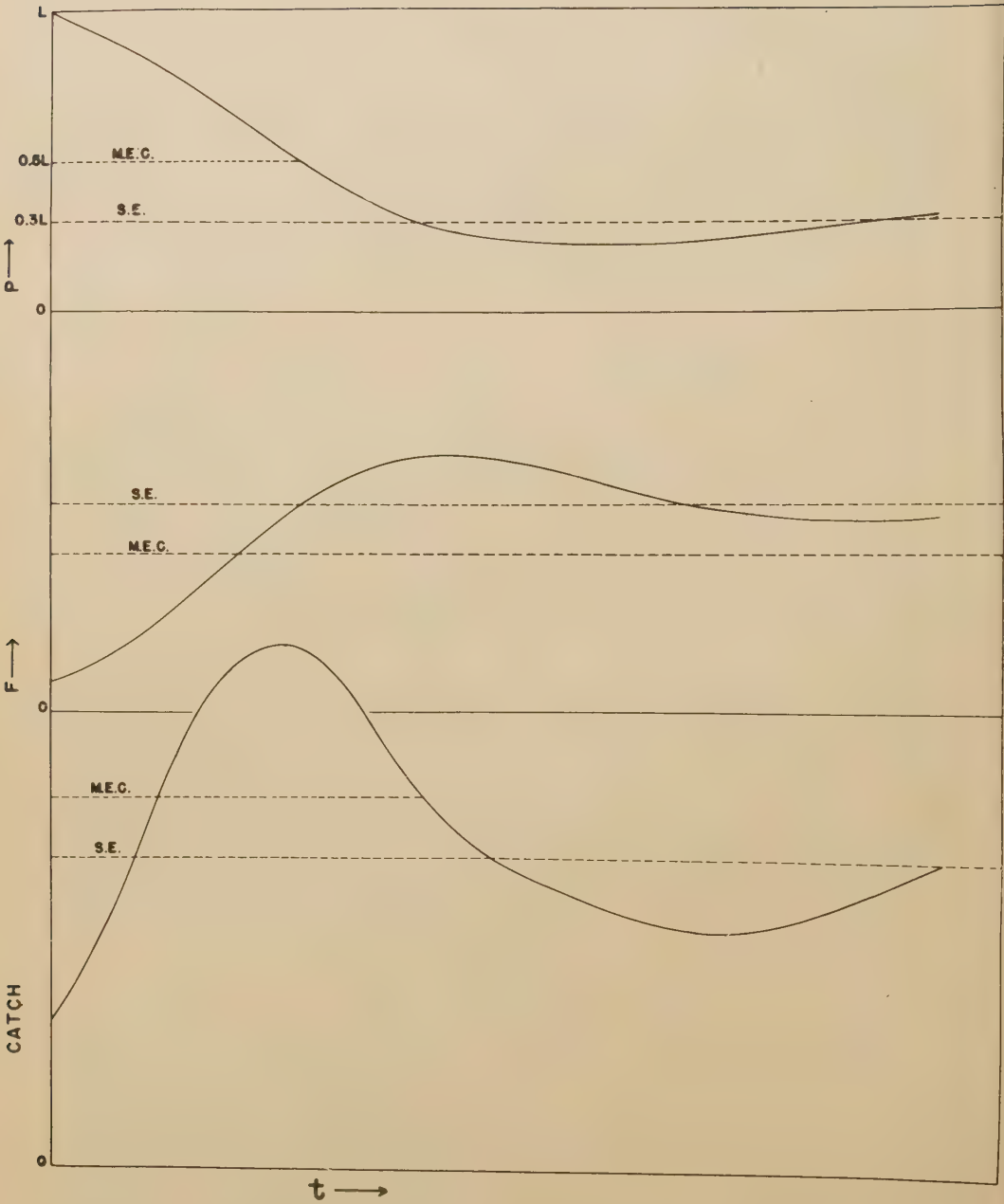


Figure 4. Solution of equations (13) for $k_1 = k_3$, $b = 0.3L$. (S.E. indicates level of stable equilibrium. M.E.C. indicates level of maximum equilibrium catch).

is indicated in the figure. The relationship between F and P is plotted in Figure 5 for the values of the two variables which have been computed for this example. It may be seen that, as was deduced, it forms a spiral winding inward toward the singular point of stable equilibrium.

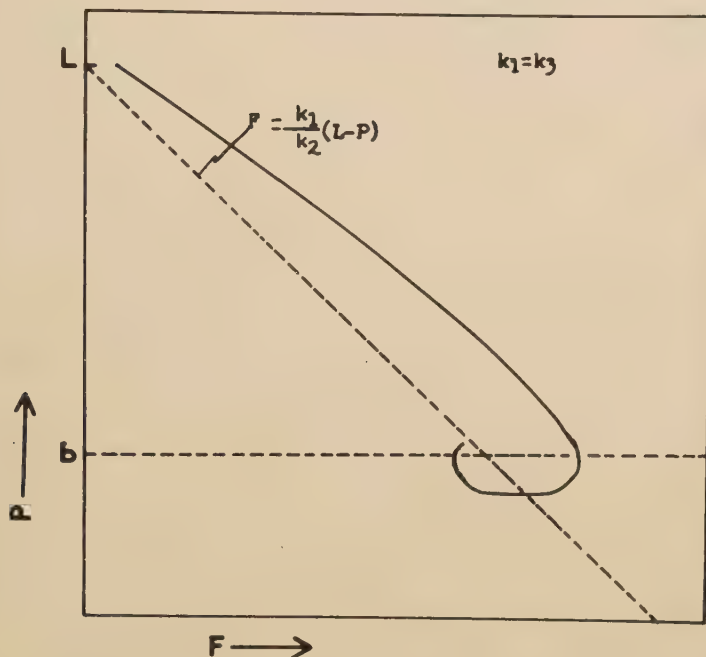


Figure 5. Solution of equations (13) for $k_1 = k_3$, $b = 0.3L$.

For the second example, for which the roots of equation (18) are real, we have taken

$$k_1 = 15k_3 \quad b = 0.3L$$

$$\text{initial conditions, } P = L \quad F = 0.1$$

The resulting solution, traced out by the method of approximation cited, showing F and P as functions of t , is graphed in Figure 6. In this case, as we expected, F and P approach the condition of stable equilibrium asymptotically from one side only. The curve of catch, however, rises well above the final stabilization level (and also somewhat above the level of maximum equilibrium catch) then approaches it asymptotically from above.

Finally, for this second example, the relationship between F and P is plotted in Figure 7, showing that its form corresponds to what we expected from the general considerations.

It is of some interest to note that Volterra and D'Ancona (1935, pp. 44-45) stated as a theorem for a system of equations which includes ours as a special case, that these two types of solutions would be found.

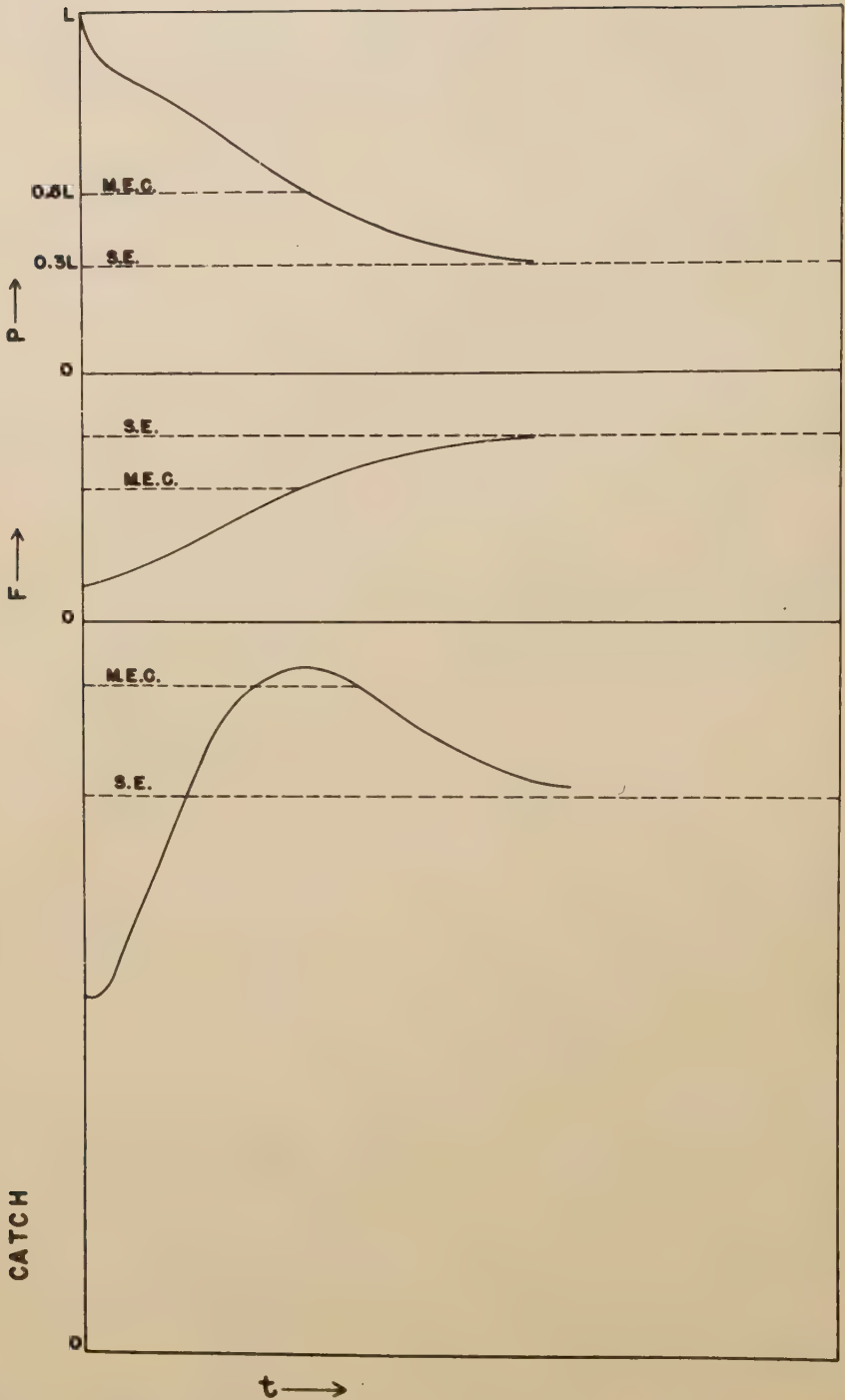


Figure 6. Solution of equations (13) for $k_1 = 15k_2$, $b = 0.3L$. (S.E. indicates level of stable equilibrium. M.E.C. indicates level of maximum equilibrium catch).

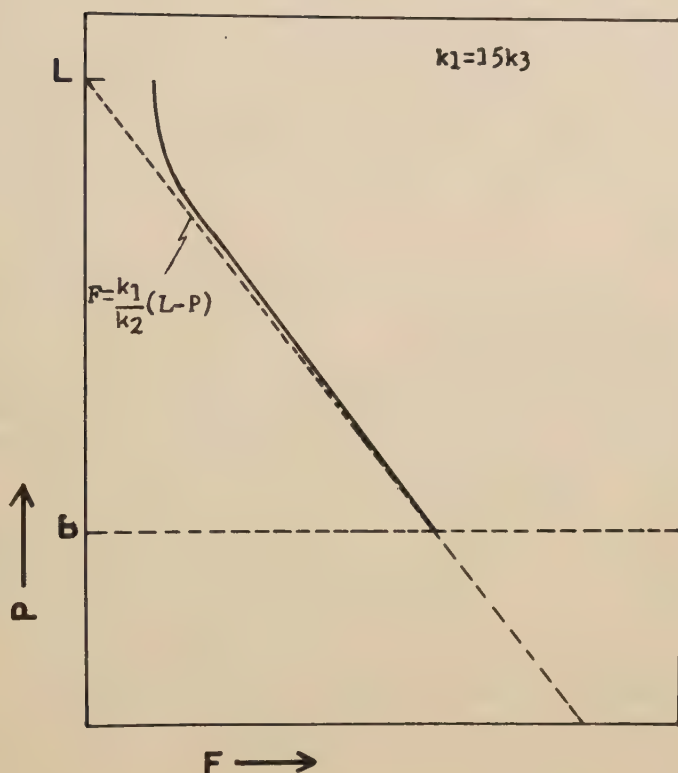


Figure 7. Solution of equations (13) for $k_1 = 15k_3$, $b = 0.3L$.

Two conclusions of importance to fisheries management follow from this analysis, if the mathematical model (13) fairly represents a commercial fishery:

- 1) Large scale fluctuations in fish population and catch can arise as a result of the interaction of the forces of growth of the fish population and growth of the intensity of fishing, with all other conditions constant.
- 2) During the development of a fishery, it is to be expected that in the course of reducing the stock of fish from its virgin condition, the catch will rise for a short time well above the level at which it will reach natural stable equilibrium, and also well above the maximum equilibrium catch. The task which conservationists have sometimes set themselves of restoring a fishery to the highest historical levels of production is, in this event, unobtainable on a permanent basis.

Examples from the commercial fisheries

It is of interest to see how well our model may be applied to the actual data of some commercial fisheries. This may be best accomplished, perhaps, by presenting the data of some well-documented fisheries in the form of Figure 5 (or 7) by plotting the observed intensity of fishing against the corresponding observed population values. It is convenient to plot U rather than $\bar{P}$, since $U = k_2 \bar{P}$, and U is the datum which is obtained directly from the statistical records of the fishery. This form has the further advantage that the product of the ordinate and abscissa for any point along the line of values of $\frac{dU}{dt} = 0$ [i.e. the line $F_t = \frac{k_1}{k_2^2} (L_u - U)$ which is equivalent to $F_t = \frac{k_1}{k_2} (L - \bar{P})$], and which we will call the line of equilibrium conditions, is the equilibrium catch.

There have been noted previously certain properties, under our theory, of this sort of diagram which should be remembered here. When $\frac{dU}{dt}$ is negative, that is when the population is declining, the catch being greater than the equilibrium catch, the values of F_t , U will fall to the right of the line of equilibrium conditions. Conversely, when $\frac{dU}{dt}$ is positive, that is when the population is increasing due to the catch being less than the equilibrium catch, the values of F_t , U will fall to the left of the line of equilibrium conditions. This property, as well as the equation of the line of equilibrium conditions depends *only* on the first equation of (13) and is completely independent of the second equation. So long as the first equation of (13) correctly describes the natural rate of increase and the catch, the line of equilibrium conditions is determined, and the properties mentioned hold regardless of the way in which F_t varies in relation to P and t . The points F_t , U will fall to the right or left of the line depending on whether the catch is greater or less than the equilibrium catch for the particular value of P .

If, *in addition*, the second equation of (13) is true, the successive values of F_t , U will form a curve corresponding to one of the joint solutions of the pair of equations, as indicated above. It should be noted here that we have assumed that the economically critical level is constant. This may be expected to be true only over a relatively limited time, since it will be influenced by technical developments as well as by the general business cycle.

We may expect the data of commercial fisheries to correspond to the properties of the model if the assumptions underlying the model are fairly well fulfilled by the fisheries. The most basic assumption was that the growth of the fish population is a function of the size of the population, and is not, therefore, subject to important variations due to other causes. If there exist other causes influencing the growth of the population of fish,

such as variations in the environment, which give rise to variations in the population growth and which are large in comparison to the changes due to population size alone, we shall expect our plot of F_t, U to exhibit a quite different pattern. In this case we should have large changes in population size in either direction quite independent of antecedent changes in the amount of fishing. As a result, the increases or decreases in population will have little orderly sequence, except as they may be related to cyclic phenomena, and will bear little relation to the location of any line of average equilibrium conditions.

Pacific Halibut

We may first consider the fishery for Pacific halibut on the Southern Grounds, which was the subject of an earlier example (p. 33). Thompson (1950, table 2) gives values of F_t and U for this fishery from 1916 through 1947. Until 1931 the fishery operated essentially without regulation of the catch or intensity of fishing, so that the population of halibut and the intensity of fishing were free to interact according to natural and economic laws. After 1931, the fishery was regulated by placing quota limits on the catch in order to build up the halibut population.

If one examines Figure 2 of Thompson and Bell (1934), in which is depicted the historical record of this fishery up to the time of regulation, it will be observed how similar the curve of landings is to our theoretical curve in Figure 4, as well as the general similarity of the curves for fishing intensity and fish population, which however, are available only for the period after the peak of the catch had been reached.

Values of F_t, U for successive years are plotted from Thompson's (1950) table 2 in our Figure 8. There has also been drawn the line of equilibrium conditions, using the values of the constants estimated by our Previous analysis (p. 36), $\frac{k_1}{k_2^2} = 4.64, L_u = 156.1$.

It may be seen that the picture is not inconsistent with the theory. From 1916 until 1930, the stock was falling and the plotted points remain generally to the right of the line of equilibrium conditions. It may be that by 1930, the stock had fallen below an economically critical level and the fishing intensity had commenced, in consequence, to decrease; however, regulation of the fishery commenced in 1931 so we cannot tell much about this. From 1932 to 1947, during which the stock was being built up, the plotted points remain to the left of the line of equilibrium conditions, approaching it closely in the last years of the series when the fishery was becoming stabilized under regulation. This corresponds to just what would be expected from the theoretical considerations discussed above.

We have also plotted on this diagram, as a light broken line, the line of equilibrium conditions corresponding to the fish population logistic with upper asymptote at $L_u = 275$, which, it will be remembered, was obtained

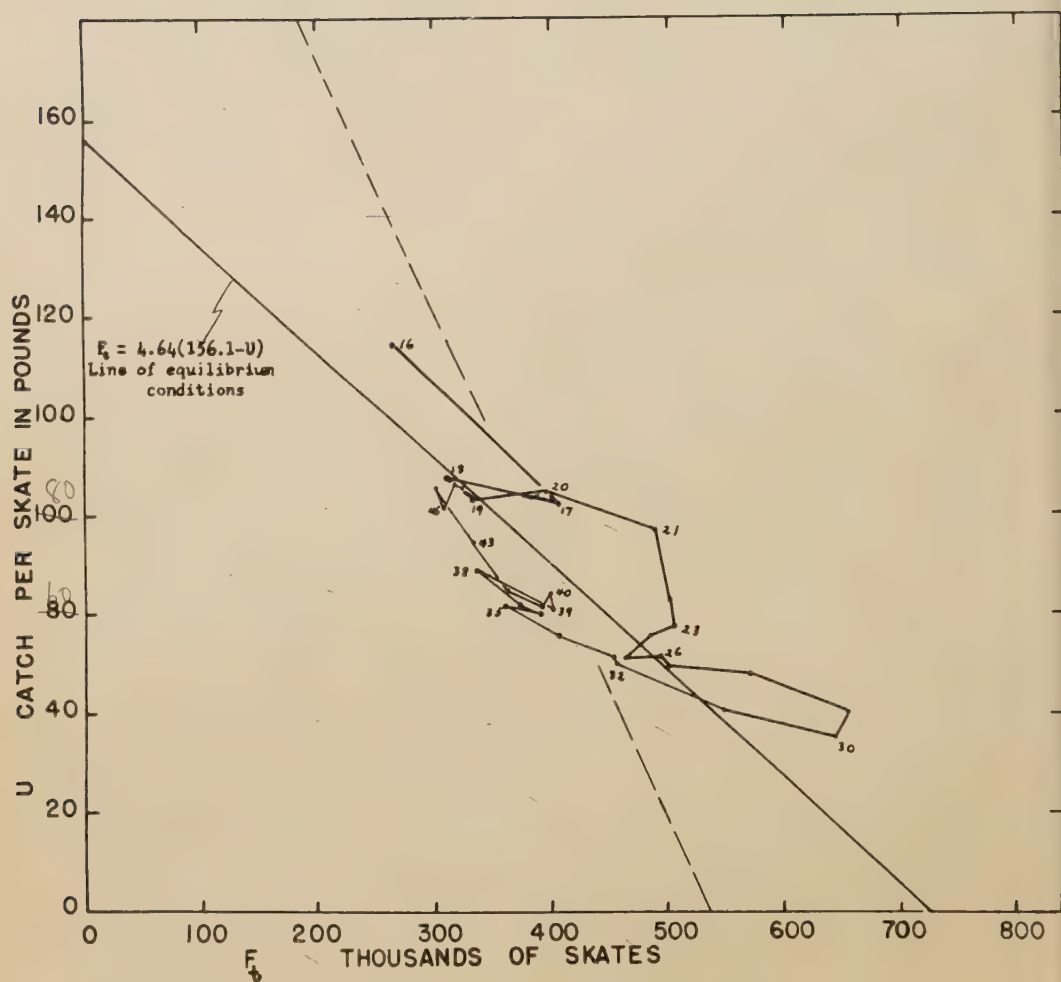


Figure 8. Relationship between intensity of fishing and mean population, Pacific halibut south of Cape Spencer.

from the data of the fishery if we specified that the curve should go through this value for $\bar{P} = L$. It may be seen that, employing this line, the plotted points do not form a very reasonable pattern in the light of the theory. It seems therefore most probable that the fish population growth curve with $L_u = 156.1$ corresponds more nearly to reality. If this line of equilibrium conditions is valid for this stock of halibut, the maximum equilibrium catch is 28.2 million pounds with a stabilized fishing intensity of 362 thousand skates. Due to lack of data at higher levels of population this estimate may not be quite correct, however, as pointed out previously.

California Sardine (Pacific Pilchard)

The fishery for the California Sardine, or Pacific Pilchard, has been the subject of much study, and of some notable differences of opinion, during the course of its growth and subsequent decline. It may be instructive to see what sort of results are obtained from considering the population statistics of this fishery in the light of the theory herein developed. In view of the widely held opinion that the major changes in the sardine population have been due to variation in environmental conditions, this is, of course, a bold attempt. In our treatment, variation due to environment is treated as a random variable, independent of P .

Statistics of total catch along the Pacific Coast are available since the early days of the fishery (Schaefer, Sette and Marr 1951, Clark 1952), but data on catch-per-unit-of-effort are available only since the 1932-33 season. The period covered by data on abundance commences, as may be seen from Figure 1 of Schaefer, Sette and Marr, after the fishery was well along in its development, but yet considerably prior to the peak of total catch. In this respect, the data are available for a period commencing when the fishery is "younger" than the initial point of the series for Pacific halibut.

Figures of total catch along the Pacific Coast were taken from Table 1 of Clark (1952). Figures of abundance (catch per California boat month linked to the base year 1941) were taken from Table 3 of Clark and Daugherty (1952). The total catch divided by the catch per boat month gives the apparent intensity of fishing in terms of 1941 California boat-months.

In order to translate values of abundance, U , into values of $\bar{P}$ we need to evaluate the constant $1/k_2$ in (9). To do this, we have referred to the results of California tagging experiments from 1936 to 1943, from which it appears that the average annual fishing mortality rate during that period was about 43 percent (Clark and Jansen 1945) for the California fishery. Using the average of the intensity of fishing in California, as given by Clark and Daugherty (1952), during the same period we have obtained $1/k_2 = 2.197 \times 10^3$ (for U in tons per boat month and $\bar{P}$ in tons). Proceeding as before (p. 33) we then estimated the equilibrium catch for each season from 1934-35 to 1949-50. Fitting a curve of the form $\bar{f}(\bar{P}) =$

where near 600 tons per boat month. From 1934 to 1937, the population was declining, the decline being associated with catches above the equilibrium catches for the corresponding population sizes. From 1938 to 1942, the pattern is somewhat confused. During this period two things transpired which may account for much of this: (1) There were unusually good year classes entering the fishery from the spawnings of 1938 and 1939 (Clark 1952, Clark and Daugherty, 1952), so that the population growth was greater than would be expected from the average relation of population size to growth of population. (2) The fishery was affected by some restrictions and disturbances at the outbreak of the war. From 1942 to 1947, the population is again rather steadily declining, with the catch above the equilibrium catch. From 1947 to 1949, the catch is below the equilibrium catch and the population is increasing. In 1950 the population again shows some decline, which is associated with a catch above the equilibrium value. From this it would appear that there may be an economically critical level near 150 tons per boat month, and if left to stabilize by itself the fishery would tend to fluctuate about the corresponding population size, at which the equilibrium catch is, on the average, about 232,000 tons per year.

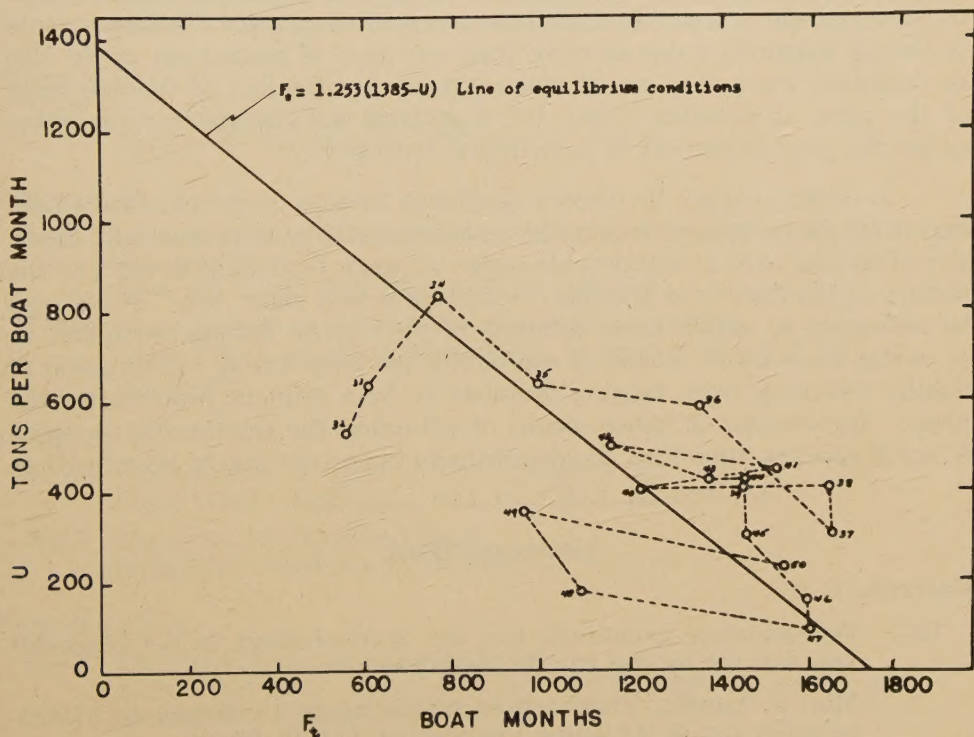


Figure 10. Relationship between intensity of fishing and mean population, California sardine.

The pattern of changes in the sardine population, then, over the period for which data are available, appears to be in general consistent with the hypothesis that one of the major causes of the changes has been the associated changes in the intensity of fishing. If the estimated line of equilibrium conditions is correct for this population, the average maximum equilibrium catch will be about 601 thousand tons at a population level corresponding to 692 tons per boat month (a mean population of about 1,520,000 tons), with a stabilized fishing intensity of 868 boat months per year.

The foregoing examples illustrate how the theory developed here may be employed to make estimates concerning the condition of a commercial marine fishery. The examples employed, although having perhaps as complete information as any available for this purpose, leave something to be desired. In particular, in both of these examples, very little or no data are available concerning intensity of fishing and abundance for the early period of development of the fishery, well before the maximum catches are reached. A great deal of precision would be added to the estimate if such information were available.

We may emphasize, therefore, the desirability of obtaining detailed information on the total catch and catch-per-unit-of-effort from as early in the development of a commercial fishery as may be possible. Measurements of fishing mortality rates at more than one level of population would also be desirable, since they would make possible verification of the adequacy of the form of equation (13a) for describing the changes in population under the joint influences of growth and fishing.

In order to apply the theory developed here to the tropical tuna fishery, it will be necessary to compile statistics of catch, abundance and intensity of fishing over a considerable series of years, beginning as early in the history of the fishery as possible. This task is well under way. It will also be necessary to obtain some estimate of the rate of fishing mortality, or to devise some other means of estimating the constant k_2 . Estimation of fishing mortality from tagging promises to be a difficult problem for the tunas. Exploration of other means of obtaining the relationship between U and P appears, therefore, to constitute an important line of investigation.

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